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Pollen Manipulation and Related Activities and Structures in Bees of the Family Apidae¹

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ABSTRACT

Pollen manipulation is described for all major groups of Apidae, and for comparative purposes, other bees are also considered. In *prototypic* pollen collecting, pollen is removed from the front legs and head, and carried in the crop. In *eutypic* pollen collecting, it is removed from the front and mid legs as well as surfaces of the head and thorax and transferred by the middle legs to the scopa on the hind legs. Different *derived* or *metatypic* types of pollen manipulation supplement the eutypic behavior and provide for transfer of pollen to the abdominal scopa in the Megachilidae and from the abdomen to the hind tibiae in the Apidae.

In Apidae the brushy scopa of many other bees is modified into a corbicular scopa, which with the hind tibial surface forms the corbicula. Corbicular filling (= pollen packing) can be

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achieved with little or no modification of cutypical behavior; for Apidae this is called Type I pollen packing, in which pollen is put directly into the corbiculae by the middle legs. Nesting materials are packed and transported in the same way. On the other hand, the corbicula is usually loaded with pollen from its distal end. This is Type II pollen packing. It may be either (a) ipsilateral, a modified eutypic pattern in which pollen is placed on the outside of the tibiotarsal joint by the middle leg of the same side, and thence pushed basad into the corbicula, or (b) contralateral, a derived pattern in which pollen transferred by the middle legs to the inner surfaces of the hind basitarsi or swept from the abdomen by those basitarsi, is transferred to the corbicula of the opposite tibia.

In pollen-manipulating movements and structures, certain Meliponinae appear to be the most primitive apids, apparently lacking Type II pollen-packing behavior as well as structures necessary for it. For other Meliponinae, ipsilateral Type II pollen packing is most important, although some have contralateral Type II behavior as part of their repertoire. The small hind basitarsus without an auricle suggests that contralateral Type II packing is of little importance in most Meliponinae, although an auricular area can function like the auricle to push pollen basad into the corbicula. Euglossini are inadequately studied, but probably exhibit ipsilateral Type II behavior. Bombini and Apinae are similar to one another in pollen-handling structure and behavior and for both, contralateral Type II pollen packing is a principal method.

Modifications of usual pollen-manipulating movements are seen in scent manipulation by male euglossine bees and in pollen-gleaning activity by certain Meliponinae (*Scaura*).

Most of the pollen-manipulation movements are either the same as self-grooming movements or are opposites of them so that, for example, a structure that is stroked distally for cleaning may be stroked basally to load it with pollen, the cleaning movement proper serving later for unloading. Presumably such loading movements are derived from similar cleaning movements. Only the hind basitarsal movements that push pollen basad into the corbicula lack counterparts in cleaning or other known behavior.

INTRODUCTION

The purpose of this paper is to describe movements whereby pollen and other materials are collected and placed for transport in the apid "pollen baskets" or corbiculae, the derivation of these movements from self-grooming behavior, and the meaning of these movements and related structures for apid evolution. Morphological and behavioral features for collecting and transporting materials play a crucial role in the evolution and adaptive radiation of the bees (superfamily Apoidea). These features are therefore important both for bee taxonomy and for evaluating homologies and convergence (Michener, 1944, 1974; Jander, 1976; Winston and Michener, 1977). While the adaptations for transport of nonliquid materials in most families of bees relate primarily to pollen, in the Apidae they are

also associated with the transport of materials used in nest construction.

The family Apidae is divided into four distinct groups, the subfamily Meliponinae (the sister group to all the rest according to Winston and Michener, 1977), the tribes Euglossini and Bombini (currently united in the subfamily Bombinae), and the subfamily Apinae. In the past, pollen-collecting behavior has been well described only for the Apinae; progressively less was known about this behavior in the Bombini, Meliponinae and Euglossini (Maurizio, 1968).

While some female bees (Euryglossinae, Hylaeinae) transport pollen to the nest exclusively in the crop, most carry at least part of their pollen harvest with the help of hairs which are located differently in the various taxonomic groups. Such hairs form the scopa, a term applied to

pollen-carrying hairs whether they are on the outer sides of the hind tibiae and basitarsi, the under sides of the basal segments of the hind legs, the sides of the propodeum, or the under surface of the abdomen (Braue, 1913; Michener, 1944). In the Apidae and the family most similar to it, the Anthophoridae, the scopa is largely restricted to the outer side of the hind tibia, a restriction unusual in other families of bees (but see the Panurginae in the Andrenidae). While the scopa is brushy in the Anthophoridae, it is reduced in the Apidae to a corbicular scopa or fringe surrounding a smooth and often concave surface on the outer side of the tibia; the fringe and surface together constitute the corbicula or pollen basket. The manner in which the corbicula is filled is the major topic of this paper; the process is sometimes called pollen packing.

In most bees which carry pollen on the scopa of the hind legs, unmoistened pollen is swept off of anthers or off the hairs of the bee's head by the front basitarsi, then transferred to the middle legs which also typically sweep pollen off the thorax. The middle legs then transfer their pollen to the scopa. These movements have been seen in halictids, andrenids, and in anthophorids as different as *Ceratina*, *Xylocopa*, *Melissodes*, and *Svastra* (R.J., personal observations). In many cases (e.g., for halictids, Michener and Wille, 1961; Batra, 1966; Roberts, 1969; for *Andrena* spp., Michener, unpublished) these movements occur while the bee is on the flower, supported by its legs, and only one leg moves at a time; the legs of a pair are not synchronized. (The repertoire of these bees may also include movements, perhaps synchronous, performed in flight; leg movements during flight have not been investigated.)

The movements for pollen handling and transport appear to be combinations and modifications of apoid self-grooming movements (Jander, 1976, and in prepara-

tion). The transfer of dirt (in grooming) is consistently from anterior to more posterior legs and it is commonly discarded from the hind legs. The same is true in the case of pollen transfer, but cleaning of the posterior legs is delayed until the bee is in its nest where it removes the pollen to be used for larval or adult food.

We have been much impressed by the well known fact that bees of the same species, no doubt often the same individuals, exhibit different pollen-collecting behavior on different kinds of flowers. The repertoire of each species is probably extensive. Therefore, conclusions about the evolution of the behavioral patterns or the phylogeny of the bees as shown by such patterns are presented with some hesitation. For example, it is always possible that a behavioral pattern thought to be restricted to a derived group of bees will be found as an uncommon pattern, or perhaps commonly with pollen of a particular consistency, in a primitive group. Nonetheless, we have interpreted our findings in evolutionary terms, we believe with justification, even though more observations will doubtless extend the known taxonomic range of some behaviors.

MATERIALS

Observations of pollen packing and related transport behavior have been made by us and by prior authors on the species listed below. Each species name is followed by the number of critical observations of pollen packing where known (in parentheses), location, and the observers (initials for the authors of the present paper) or literature references.

MELIPONINAE:

Trigona (Trigonica) buysoni (6); Rio Anchicayá, Prov. del Valle, Colombia, collecting pollen from *Hedychium coronarium* (C.D.M.).

Trigona (Paratrigona) impunctata (10); 7.5 km southwest of Kourou, French Guiana, collecting pollen from a large-flowered *Cassia* (C.D.M., M.L.W.); 6 km southwest of Kourou, French Guiana, collecting

pollen from *Stylosanthes* (C.D.M.); 12 km southwest of Kourou, French Guiana, collecting pollen from melastomaceous shrub (C.D.M.).

Trigona (*Paratrigona*) *subnuda*; State of Paraná, Brazil, collecting pollen from *Tibouchina* spp. (Laroca, 1970).

Trigona (*Paratrigona*) sp.; Pichinde, Prov. del Valle, Colombia, on flowers of *Baccharis* (?) (C.D.M.).

Trigona (*Scaptotrigona*) *pectoralis*; Pichinde, Prov. del Valle, Colombia, on flowers of *Baccharis* (?) (C.D.M.).

Trigona (*Scaptotrigona*) *postica*; Rio Claro, São Paulo, Brazil, collecting cerumen from old *Trigona* nest (Sakagami and Camargo, 1964).

Trigona (*Cephalotrigona*) *capitata* (10); 6 km southwest of Kourou, French Guiana, collecting pollen from *Stylosanthes* (C.D.M.).

Trigona (*Tetragona*) *clavipes* (8); Kourou, French Guiana, collecting pollen from white *Ipomoea* (C.D.M., M.L.W.).

Trigona (*Tetragona*) *fimbriata*; near Kuala Lumpur, Malaysia, 10 specimens with pollen loads, no behavioral observations (C.D.M.).

Trigona (*Tetragona*) *jaty*; Costa Rican colony introduced to laboratory at Lawrence, Kansas, by E. M. Barrows, collecting pollen from *Prunus* (R.J.).

Trigona (*Tetragona*) *thoracica* and *itama*; Kepong near Kuala Lumpur, Malaysia, collecting pollen from *Cassia spectabilis* (R.J.).

Trigona (*Trigona*) *amalthaea* (= *trinidadensis*) (10); highway summit west of Cali, Prov. del Valle, Colombia, collecting pollen from *Cucurbita pepo* (C.D.M., M. D. Breed, W. J. Bell).

Trigona (*Trigona*) *fulviventris fulviventris*, *fuscipennis*, and *silvestriana*; Prov. de Guanacaste, Costa Rica, collecting pollen from *Cassia biflora* (Wille, 1963).

Trigona (*Trigona*) *nigerrima* (many); Rio Anchicayá, Prov. del Valle, Colombia, collecting pollen from *Hedychium coronarium* (C.D.M., M. D. Breed; cinematography by M. D. Breed).

Trigona (*Trigona*) *pallida* (many); Kourou, French Guiana, collecting pollen from white *Ipomoea* (C.D.M., M.L.W.); 7.5 km southwest of Kourou, collecting pollen from a large-flowered *Cassia* (C.D.M., M.L.W.).

Trigona (*Trigona*) *spinipes* and *fulviventris guianae*; State of Paraná, Brazil, collecting pollen from *Tibouchina* spp. (Laroca, 1970).

Trigona (*Trigona*) *fulviventris guianae*; 12 km southwest of Kourou, French Guiana, collecting pollen from melastomaceous shrub (C.D.M.).

Trigona (*Scatra*) *latitarsis*; State of Maranhão, Brazil, collecting pollen from *Piper* and *Amaranthus* (Laroca and Lauer, 1973).

Trigona (*Scatra*) *longula* (10); 7.5 km southwest of Kourou, French Guiana, collecting pollen from a large flowered *Cassia* (C.D.M., M.L.W.).

Melipona fasciata and *furva*; French Guiana, fresh specimens with pollen loads of various sizes (M.L.W.). Loading behavior not observed because of rapid flight.

Melipona fasciata; Osa Peninsula, Costa Rica, collecting mud (R.J.).

Melipona pseudocentris; 12 km southwest of Kourou, French Guiana, collecting pollen from melastomaceous shrub (C.D.M.).

EUGLOSSINI:

Englossa cordata group and *E. ignita* (20); 49 km south of Cayenne and 19 km southwest of Kourou, French Guiana, collecting pollen from *Sabicea* near *cinezea* (C.D.M., M.L.W., G. Otis).

Englossa cordata group (2); Kourou, French Guiana, collecting cerumen from an old *Trigona* nest (C.D.M.).

Englossa cordata group (10); vicinity of Kourou, French Guiana, males collecting cincole and other scents (C.D.M.).

Englossa championi (many); Rio Anchicayá, Prov. del Valle, Colombia, males collecting cincole and other scents (C.D.M., M. D. Breed; cinematography by M. D. Breed).

Eulaema cingulata (1) and *Euplusia auripes* (2); vicinity of Kourou, French Guiana, males collecting cincole and other scents (C.D.M.).

BOMBINI:

Bombus spp.; Europe, pollen collecting (Hoffer, 1882; Sladen, 1911, 1912a; Buttel-Reepen, 1915).

Bombus cayennensis; 45 km southwest of Cayenne, French Guiana; fresh specimens with pollen loads (C.D.M.).

Bombus pennsylvanicus (= *americanorum*); Baldwin, Kansas, pollen collecting on *Cassia chamaecrista* (observations and cinematography by R.J.).

APINAE:

Apis mellifera; Europe and North America, pollen collecting (Sladen, 1912b; Parker, 1926; Beling, 1931; Ribbands, 1953; Snodgrass, 1956; Legge and Bole, 1975); Lawrence, Kansas, pollen collecting on *Cytisus scoparius* (R.J.); Europe, Brazil, resin (propolis) collecting (Sladen, 1911, 1912b; Röscher, 1927; Meyer, 1953, 1954, 1956; Sakagami and Camargo, 1964); Lawrence, Kansas, resin (propolis) collecting (observations and cinematography by R.J.).

METHODS

Behavior while a bee is on a flower is usually easily observed, but much of the pollen manipulation in the Apidae occurs in flight. Certain individuals, especially of the genus *Trigona*, hover briefly and rather quietly close to the flowers, and can be watched against the background of the flowers when desired. They then often return to the same flower for more pollen, and repeat the hovering. Such individuals are the principal sources of our new data on leg movements. Considerable detail was visible and the behavior pattern was pieced together from observations of many different hovering individuals, mostly of *Trigona pallida* and *nigerrima*, from all possible

angles. C.D.M. and M. D. Breed observed pollen manipulation by *Trigona* as well as leg movements of male euglossine bees in southwestern Colombia; Dr. Breed made moving pictures which were later analyzed by C.D.M., R.J. made moving pictures of resin collecting by *Apis mellifera* and of pollen collecting by *Bombus pennsylvanicus*. The films were analyzed with the invaluable help of a Super 8 Lafayette Analyzer Projector.

Another source of information is pollen on the legs of bees killed while collecting pollen. The anatomical details and the location of pollen accumulation help in determining the packing behavior. These data, collected by C.D.M. and M.L.W. and recorded largely as sketches and notes made at Kourou, French Guiana, usually substantiate the behavioral data.

Various behavioral matters that are not directly related to filling the corbiculae are mentioned in passing. To save space, references in such cases are not usually included, but can be found in Michener (1974).

The terminology used for the movements involved in pollen manipulation is that of Jander (1976). In *rubbing*, two parts move back and forth, one against the other, without losing contact throughout the action. In *scraping*, strokes in one direction involve contact, but the parts are separated for the return strokes. For hairy structures such as many bees have, these terms may not seem ideal; words like brushing or combing are more descriptive. However, they do not indicate the distinction drawn between rubbing and scraping and are avoided except when our observations are not good enough to make that distinction.

Oriental terms for the legs, especially for movements relative to the hind tibia, can be confusing. In the tibia's usual position, upward might be regarded as toward the base. Because it is moveable, that usage is avoided, and we use instead *basad*, toward the base or femoral articulation, and *apicad*, toward the apex. These are simply directional terms; a basad movement can occur near the apex of the tibia. Because the tibia is often extended posteriorly, *upward* is taken to be toward the upper margin, i.e., at right angles to the long axis of the tibia. The same direction relative to the tibia can be called *posterior* if the long axis of the tibia is considered to be vertical.

TRANSPORT OF NESTING MATERIALS

Species of *Melipona* are regularly seen collecting mud and carrying it in the corbiculae, and *Melipona* and *Trigona* both carry cerumen from other nests, as well as gums and resins, in a similar way. Some species of *Trigona* also carry vertebrate fecal material, mud, or chewed plant ma-

terial in the corbiculae. Bassindale (1955) gives an account of propolis packing by *T. braunsi* and Sakagami and Camargo (1964) illustrate and give an account of the similar packing of cerumen for transport by *T. postica*. The latter authors report that the mandibles cut out particles of cerumen which are manipulated and pressed together to form a lump by the mandibles and forelegs (probably basitarsi, C.D.M.). "When the lump attains an appropriate size, one of the middle legs reaches forward, and using bristles on its underside (basitarsus? C.D.M.), the bee transfers the lump very rapidly to the corbicular surface of the hind leg of the same side, which is synchronously moved a little forward." By repetition of these movements, the accumulation on the corbicula grows. Often the middle leg is extended back, and gently presses the growing ipsilateral (same side) corbicular deposit. One or both of the hind legs may be raised in a peculiar way above the wings; the function of this movement, if any, is unknown.

One of us (R.J.) has observed collecting and transport of mud by *Melipona fasciata*. Biting with the mandibles and scratching with the forelegs, the bee loosens a bit of moist mud, which is then taken up by the mandibles. With a backward motion, one foreleg takes the bit of mud from the mandibles. The ipsilateral middle leg scrapes the piece of mud from the foreleg by claspings the foreleg from the outside. This movement appears identical to the cleaning of the foreleg by the middle leg during a normal cleaning bout (Jander, 1976). The middle leg then passes the mud backward and presses it from the outside into the corbicula. This is usually followed by patting movements of the middle leg on to the mud in the corbicula. Only unilateral (one side at a time) transfer of mud was observed; mud may be passed backward on one side several times

before the bee uses the other side. After both corbiculae have been filled, but before taking flight, the bee takes a larger lump of mud between the mandibles, first holding it with both forelegs and then pressing it to the mandibles.

Euglossa and *Euplusia* carry resin in the corbicula and *Eulaema* carries vertebrate fecal material as well as resin. *Euplusia* sometimes carries small pieces of bark stuck to the resin, if museum specimens with such bark are meaningful. One female of the *Euglossa cordata* group was observed taking cerumen from fragments of an abandoned *Trigona* nest. Few observations were possible, so that details are not available, but the bee clearly detached pieces of cerumen with its mandibles, then hovered and while in the air transferred the cerumen to the corbiculae. The middle legs clearly were seen to synchronously carry pieces back to the ipsilateral hind legs which were brought forward, the middle legs then patting the cerumen into the corbiculae. The bee then alit to obtain more cerumen. The cerumen masses on the corbiculae became large and irregular. Because of behavior in other groups as well as in euglossine males described below, we suspect that euglossines may not always hover to transfer sticky materials to the corbiculae synchronously with both middle legs. Non-flying Meliponinae and Apinae have been seen to transfer sticky materials to the corbiculae asynchronously, with one middle leg at a time.

Bombus constructs its nests using a mixture of wax and pollen. Wax is secreted by the bees. So far as known, pollen is not transported differently for construction than for food; in fact young larvae may eat some of the wax-pollen mixture. Transport of pollen is described below.

Apis mellifera, both in Europe and the Africanized bees in Brazil, collects resin (propolis) or cerumen exactly as described

above for *Trigona postica* except that the hind legs are not raised (Sladen, 1912b; Rösch, 1927; Meyer, 1953, 1954, 1956; Sakagami and Camargo, 1964; see IBRA, 1976). One of us (R.J.) made additional observations of such behavior, summarized as follows: The mandibles gnaw the surface of the resin while at the same time the forelegs and occasionally the middle legs scrape and scratch the surface. Loosened pieces are released by the mandibles to both forelegs. In a very quick movement, one foreleg swings backward and the ipsilateral middle leg grasps the foreleg from the outside and scrapes off the propolis. The femorotibial joint of the middle leg is sharply bent in this operation (as when the middle leg cleans the foreleg in grooming, Jander, 1976) and the piece of propolis sticks to the inner posterior side of the mid basitarsus, presumably held by the sharp bristles in that area. Immediately the middle leg swings backward and the piece of propolis is pressed by the mid basitarsus onto the corbicula of the ipsilateral hind leg. Then the middle leg is pulled forward while still in contact with the hind leg; the resultant scraping movement leaves the resin in the corbicula. The pressing and scraping may then be repeated a second time. All these movements were performed while the bees were on the ground.

MANIPULATION OF SCENTS BY MALE EUGLOSSINI

Male euglossine bees collect certain scented substances from orchid flowers and other sources (Vogel, 1966) and can be attracted to scents provided artificially (Dodson et al., 1969). Interestingly, the movements involved are similar to those of pollen collecting by females, although other male bees, so far as known, use similar movements only for self-grooming. Several species were observed; the following observations apply equally to *Euglossa*, *Euplusia*, and *Eulaema*, and largely support

the detailed accounts and illustrations by Vogel (1966) and Evoy and Jones (1971). (The middle tibia cited by the latter authors appears to have been in reality the middle basitarsus.)

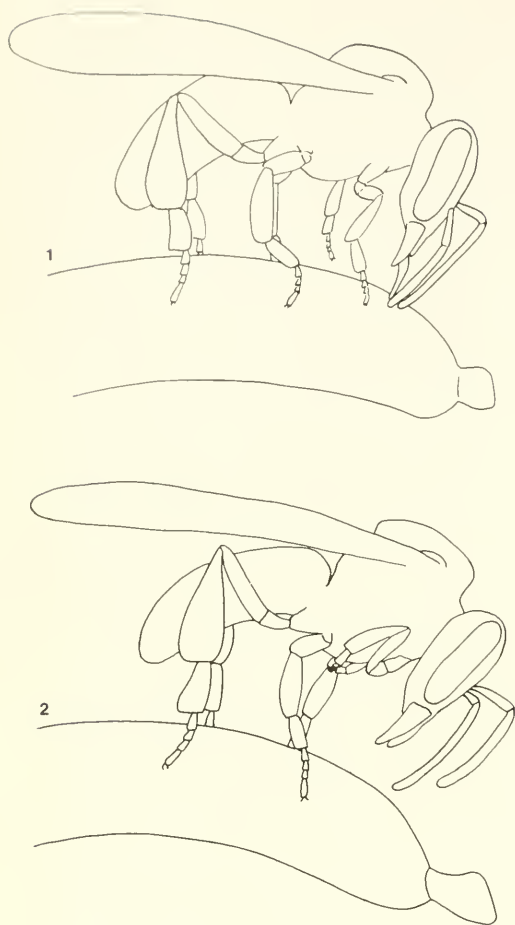
The front tarsi are rubbed on the material containing the attractant; sometimes they also scrape the head, especially the eyes, downward and forward as in grooming movements. The proboscis is not exerted; the tips of the antennae are directed down to or almost to the scent source. After such rubbing, the bee usually hovers and while in the air the middle legs move forward synchronously and apparently scrape the fore tarsi with the under surfaces of the ipsilateral mid basitarsi. The middle leg is probably flexed as in normal cleaning of the foreleg. The middle legs now move back, and at the same time the hind legs are synchronously flexed and rotated forward. Now the under surfaces of the mid basitarsi scrape synchronously upward, i.e., at right angles to the long axes, across the outer surfaces of the enlarged hind tibiae. The two structures are nearly parallel to one another, and only at the end of each stroke may the mid basitarsus contact the hairs of the dorsal metatibial groove. The whole sequence is repeated several times while the bee is hovering, before it alights again at the source of the scent, or departs. The greater part of the contact of the middle tarsus with the hind tibia is with the simple, convex, short-haired, outer, tibial surface and not with the groove which is supposed to absorb the attractant substances.

Rarely, instead of hovering, a bee grasps the edge of a leaf with its mandibles after rubbing an attractant with its front tarsi, and then, hanging by the mandibles, it goes through the leg movements described above. It thus frees the middle and hind legs for the movements usually performed while hovering.

APID POLLEN MANIPULATION

THE FORELEGS. As in most other bees, the front legs (basitarsi) and the proboscis remove pollen from the anthers of flowers; pollen on the proboscis and the head is subsequently scraped off by the forward and downward movements of the front legs. Thus for most species at most kinds of flowers, the front legs are particularly important, being the primary pollen gathering structures. Pollen is generally transferred backward directly from the front legs to the middle legs (basitarsi), which also clean pollen from both dorsal and ventral surfaces of the thorax. However, these movements in the meliponine genus *Trigona* are unusual, as described below.

In flowers whose anthers are readily accessible, *Trigona* species commonly bite an anther repeatedly, loosening pollen, the antennae being bent down, their tips contacting the anther or nearly so. If there is already loose pollen, biting is unnecessary. At least *T. capitata*, *pallida*, *thoracica*, and *nigerrima*, and presumably all species, extend the proboscis, contacting the anthers repeatedly (Fig. 1). The pollen is presumably made sticky with nectar in this way, as is the case with *Apis*. As these activities continue, bees brush the anthers and especially the proboscis with the front tarsi, presumably accumulating pollen on the hairs of the basitarsi. The proboscis is scraped downward, toward its apex, with both forelegs (basitarsi?) synchronously. The pollen is then transferred by the front tarsi to an area of backward-directed, stiff hairs on the ventral surface of the mesepisternum in front of and between the middle coxae, and to similar hairs on the middle and hind coxae. These movements are synchronous, left and right forelegs moving simultaneously, the bee being supported by the middle and hind legs (Fig. 2). Moving pictures show that the fore tarsi are scraped forward across the coxal



FIGS. 1, 2. *Trigona nigerrima* taking pollen from *Hedychium*. In Fig. 1, in an interval between biting, the tip of the glossa is in contact with the pollen source and the forelegs are about to scrape the glossa and floral surface. In Fig. 2 the forelegs are transferring pollen to the thoracic venter and mid and hind coxae. These drawings are based on moving picture frames, but much detail has been added since they showed mainly silhouettes.

and mesepisternal vestiture to transfer pollen to the latter.

The behavioral repertoire of *Trigona* species must include somewhat different movements for flowers with loose pollen that does not need to be freed with the mandibles and that may be picked up by parts of the body and appendages other than the front tarsi. When *Trigona* species

are foraging at flowers with abundant loose pollen that adheres to the body, it is no doubt brushed off of the different parts of the body by the inner surfaces of the basitarsi of all the legs. *T. pectoralis* and *T. (Paratrigona)* sp. collecting pollen on *Baccharis* (?) flowers had pollen densely caked on the inner sides of the hind basitarsi. Such pollen would never be transferred to the thoracic venter, but must pass directly to the corbicula. This is in contrast to our observations on *T. pallida* and *nigerrima* which had little pollen on the hind basitarsi.

POLLEN PACKING. We recognize two basic types of pollen packing in Apidae. Type I resembles the manipulation of nest materials, as described above, in that sticky masses are placed directly onto the corbiculae by the middle legs. In Type II, pollen is placed near the distal end of the corbicula rather than directly on the corbicular surface, and is then pushed basad into the corbicula. Special morphological features of the distal end of the hind tibia and base of the basitarsus are necessary for Type II pollen manipulation; these features differ among the groups of Apidae, as do the pollen-packing movements. There exists, therefore, various subtypes of Type II.

TYPE I POLLEN PACKING. It may be that all female apids retain, as part of their behavioral repertoire, pollen packing in which the middle legs place pollen directly into the corbiculae, as noted below for *Trigona (Trigonisca) buyssoni* and for *T. amalthea* on *Cucurbita*. For the former species this may be the principal method. It was observed on the same flowers where *T. nigerrima* was transferring pollen in the way more common for the Apidae (Type II). Most species probably use Type I packing only for large masses of sticky material such as resin, mud, or the large pollen masses of *Cucurbita*.

Trigona (Trigonisca) buyssoni bites the anthers of *Hedychium*, moistens the loosened pollen with nectar (?) from the glossa, and places it on the mesepisternum with the fore tarsi, as described above (under The Forelegs) in greater detail for other *Trigona* species. Then, while still standing on the anther or petal, supported by front and hind legs, the middle legs move pollen from the thoracic venter to the corbiculae. (The front legs could theoretically play a role in removing pollen from the thoracic venter, but if so, it must be one front leg at a time rather than synchronously since at least one front leg must support the body. Nothing of the sort was seen.) Movement of the middle legs is synchronous, and the pollen is scraped or patted onto the ipsilateral corbiculae by the middle basitarsi.

The abundant, coarse, sticky pollen of *Cucurbita* probably presents special problems or opportunities for bees collecting it. Our observations were made on *Trigona amalthea*, a form very close to and perhaps conspecific with *T. silvestriana* whose Type II handling of *Cassia* pollen has been observed by Wille (1963). But on *Cucurbita*, after several transfers of pollen (like those described under The Forelegs) from the anthers or from thick accumulations on the corolla beneath the anthers to the mesepisternum and adjacent coxae, the bee, while still in the flower and now supported by front and hind legs, uses the middle basitarsi to remove pollen masses from the mesepisternum and pat them onto the ipsilateral corbiculae. The result, after several such movements, is large but loose and irregular pollen masses on the corbiculae. The movements are similar to those of *T. postica* described by Sakagami and Camargo (1964) for placing cerumen on the hind tibiae for transportation. These movements make no use of the special structures (penicillum, rastellum) at the apices of the tibiae.

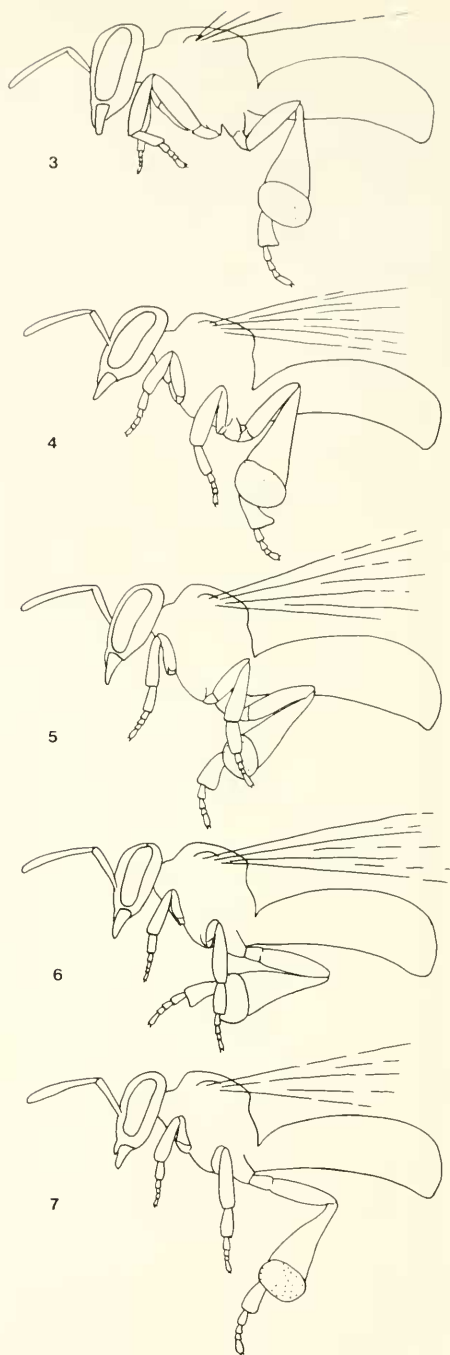
An old report (Hoffer, 1882) says that pollen is "pressed with the middle legs into the corbicula of the hind leg" by *Bombus*. This may indicate that Type I behavior is part of the repertoire of *Bombus*, as it is of other groups.

Even in *Apis mellifera*, when the corbicular pollen loads become large, the bee may pat them many times with the ipsilateral middle legs, probably to smooth and compact them. Some pollen may be added directly to the corbicular pollen masses in this way, although the quantity appears to be small (Parker, 1926).

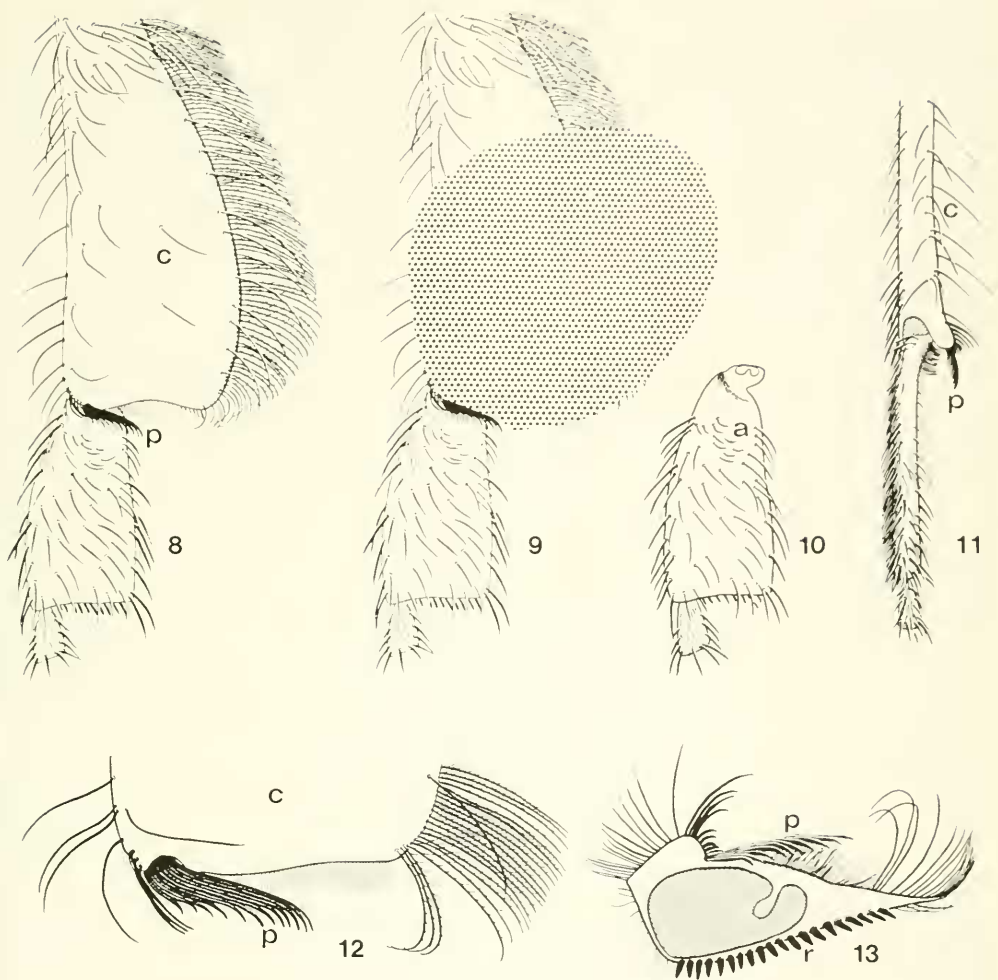
TYPE II POLLEN PACKING. This type of pollen packing involves (a) placement of sticky pollen in the region of the hind tibiotarsal joint by movements which depend upon the kind of bee and the kind of flower, and (b), most characteristically, pushing the pollen basad up the outer surface of the tibia from the region of the tibiotarsal joint. This movement of the pollen places it into the smooth and nearly hairless corbicula. This is unlike the filling of the scopa of other families of bees, where the dense scopal hairs prevent such a process, and it is unlike the Type I apid process in which pollen is placed directly into the corbicula by the middle leg. As described below, in *Apis*, *Bombus*, and probably the Euglossini, pollen is pushed basally into the tibial corbicula by the auricle, i.e., the broadened base of the basitarsus. As emphasized by Buttel-Reepen (1915), Maidl (1934), and Winston and Michener (1977), Meliponinae have no auricle. A major objective of this study, therefore, was to learn how Meliponinae fill their corbiculae.

Ipsilateral Type II Pollen Packing. Corbicular loading was observed for *Trigona pallida* and *nigerrima*, and has been briefly described for other species by Wille (1963) and Laroca (1970). After several foreleg movements that place pollen on the thoracic venter (Figs. 1 and 2), the bee

takes wing, thus freeing the middle and hind legs of their supporting function and enabling them to make pollen-transferring motions. While the bee is hovering, the middle legs synchronously rotate far forward (Fig. 3) and may scrape backward over the thoracic venter, removing pollen from the hairs of that area. However, in their far forward position they hide the front legs so that it is difficult to see, and photographs do not show, whether or not the front legs first remove the pollen from the mesepisternum and transfer it to the mid legs, as stated by Wille (1963) and Laroca (1970). Our impression from the moving pictures is that both may happen, the forelegs scraping pollen perhaps from median ventral areas for transfer to the mid legs, and the latter removing pollen from the lateroventral areas. In any event the mid legs quickly rotate back (Fig. 4) from a far forward position to a backward position and transfer pollen to the ipsilateral hind legs. At first the mid tibia and tarsus come back almost parallel to the hind tibia (Fig. 5), but then the hind leg is flexed forward (Fig. 6) so that the mid basitarsus lies across the outer surface of the tibia or the tibio-basitarsal joint of the hind leg, at right angles to the long axis of the hind tibia. The movement of the hind leg is especially noticeable in hovering *T. clavipes* and *nigerrima* because of the long and dark posterior legs, but it occurs in all species and is necessary if the contact is to be at right angles to the hind tibial axis. The position of the mid leg against the outer surface of the apex of the hind tibia shows repeatedly in our moving pictures of *T. nigerrima* hovering while manipulating pollen. Straightening of the hind leg (Fig. 7) and to a minor extent, simultaneous forward movement of the mid leg combine to scrape the pollen-carrying mid basitarsus across the apex of the hind tibia. The photographs show that sometimes the mid basitarsus is also



FIGS. 3-7. *Trigona nigerrima* packing pollen while hovering near *Hedychium* flowers. Fig. 3, Mid leg has removed pollen from thoracic venter or possibly foreleg. Fig. 4, Mid leg moving quickly backward. Fig. 5, Mid leg over pollen mass (dotted) on hind leg. Fig. 6, Hind leg bent forward so that mid leg lies across tibiotarsal joint. Fig. 7, Hind leg straightened and mid leg moved forward, pulling mid tarsus across hind leg. Drawings prepared as for Figs. 1, 2.



FIGS. 8-13. Hind leg of worker of *Trigona pallida*. Fig. 8. Tibia and basitarsus. Fig. 9, Same with large pollen mass. Fig. 10, Basitarsus showing basal structure. Fig. 11, Tibia and basitarsus in anterior view. Fig. 12, Apex of tibia, outer view. Fig. 13, Distal view of apex of tibia. p, penicillum; r, rastellum; a, auricular area; c, corbicula.

seemingly pressed against the pollen mass in the corbicula. This could be either adjustment of the pollen mass or a Type I addition of pollen, but the arrangement of pollen from different sources suggests the former (see section on The Corbicular Pollen Load in Meliponinae).

The pertinent hind tibial and basitarsal structures of *Trigona pallida* are shown in Figures 8 to 13. The penicillum is a row of stiff bristles arising on the lower (or anterior) distal angle of the tibia. They sweep upward (or posteriorly) parallel to the tibial apex, but well separated from it,

and then curve distad at their tips. The longest bristles are the outermost while those nearer the corbicular surface are progressively shorter (not true of all species). The hind basitarsus except at its tibial articulation is offset mesally (Fig. 11), so that there is a gap between its outer surface and the curved apices of the bristles of the penicillum. The structure suggests that through this space the ipsilateral middle basitarsus is drawn at right angles to the long axis of the hind tibia in order to transfer pollen onto the latter. The apices of the penicillar bristles would scrape the

pollen out of the hairs on the outer surface of the mid basitarsus, and the penicillar curvature, during posterior movement of the hind tibial apex relative to the mid basitarsus, would force such pollen basad onto the outer surface of the tibia. The progressive shortening of the penicillar bristles from the outer to the inner ones makes the comb oblique, tending to push the pollen against the apex of the corbicula. Thus the movement of hind leg relative to the middle could alone be responsible for pushing some pollen basad into the corbicula.

The posterior basal area of the outer surface of the hind basitarsus is provided with hairs which are directed posterobasally (Fig. 10), not apically like most other hairs. We speak of this part of the basitarsus as the auricular area because of its location, comparable to that of the auricle of other subfamilies of Apidae. The hairs of the auricular area often have some pollen on them and presumably serve to scrape pollen off of the inner hairs of the ipsilateral middle basitarsus. Laterad movement of the hind basitarsus would press the mid tarsus between the penicillum and the posterior basitarsus itself (including the auricular area) as the hind tibial apex is moved backward relative to the mid leg. Posterior flexion of the hind basitarsus would then help to push pollen that comes off onto the auricular area up onto the corbicula, thanks to the direction of the hairs in that area.

As repeated passages of the mid basitarsus add pollen to the distal end of the ipsilateral outer tibial surface (supplemented by the pollen from the inner surface of the contralateral hind basitarsus, see below), the added pollen must pile up and be pushed basally. The motive forces are presumably the scraping movement of the hind leg along the mid leg as already described, supplemented by back and front (up and down) flexions of the basitarsus.

Examination of freshly killed pollen collectors of *Melipona* and *Trigona* frequently show pollen on the tibial apex in the space between the inner side of the penicillum and the outer sides of the basitarsus and rastellum. In *T. pallida* a small brush (Figs. 10 and 11) arising along a curved line on the basal part of the auricular area, behind the penicillum, can, with backward flexion of the basitarsus, push such pollen basad onto the corbicular surface. It consists of weak hairs hardly able to move the whole pollen mass, but its effectiveness with small amounts of pollen was shown by drawing a detached middle tarsus with pollen on it through the gap described above (between the penicillum and the hind basitarsus) on the hind leg of a freshly killed worker of *T. pallida*. Part of the pollen was combed off as expected by the penicillum, but the quantity was not enough for the curvature of the penicillum to push much pollen basad onto the corbicula. The basitarsus was then flexed backward, with the result that the brush moved the pollen onto the distal end of the corbicula where it remained, held by its stickiness. In *Melipona*, as in most *Trigona*, there is no defined brush, but rather a hairy auricular area (Fig. 14) with hairs directed posterobasally, as described above. The frequent presence of small amounts of pollen on this area in *Melipona* and *Trigona* suggests its importance in pushing pollen upward. Such movement is possible because of the highly flexible tibiotarsal joint, activated at least in *Apis* (Snodgrass, 1956) by three muscles.

A casual observer might suspect from the curvature of the penicillar bristles that the penicillum must somehow function as a scoop, accumulating material on its concave surface. Actually if our interpretation is correct, the penicillum scrapes pollen onto its convex surface. Like the rastellar bristles in *Apis*, the penicillar bristles comb in the direction of the apices of the hairs

from which they are removing pollen. Such scraping movements can remove indefinite amounts of pollen because new pollen easily pushes away that already present. This would not be the case for a scoop.

Contralateral Pollen Packing in Apis and Bombus. Although it largely occurs while the bees are in flight, the process of pollen manipulation and packing onto the corbiculae for transport has been studied repeatedly for *Apis* (for references, see Ribbands, 1953; Snodgrass, 1956, and Legge and Bole, 1975). Sladen (1912a) and Buttel-Reepen (1915) found the process for *Bombus* to be similar, and the structures involved in *Apis* and *Bombus* are remarkably similar. The following comments are based primarily on published material on *Apis mellifera*. The bees gather pollen from their hairy bodies or from anthers by movements of the legs. At the same time, they may moisten it with nectar, making it sticky. The basitarsi bear the primary brushes involved. The front basitarsi brush both anthers and the proboscis, the latter adding nectar and making the pollen sticky. These basitarsi also brush the head and front of the thorax. R.J. observed *Apis* workers taking pollen from flowers of *Cytisus* directly with the middle, rather than the front tarsi, and bees on flowers with loose pollen will have accumulated pollen on most parts of the body and legs. The bee now leaves the flower and hovers. Pollen on the front basitarsi is transferred to the middle ones, which also scrape pollen off of much of the thorax both dorsally and ventrally. The middle basitarsi, one at a time (Beling, 1931), are now scraped between the inner sides of the apposed hind basitarsi. These basitarsi also scrape pollen off of the abdomen. The hind legs are rapidly rubbed against one another in a pumping motion. In this process the rastellum scrapes distad, removing pollen from the inner surface of the contralateral basitarsus. The pollen ac-

cumulates on the posterior basal projection (auricle) of the basitarsus or between the auricle and the rastellum. Then, by posterior (upward) flexion of the basitarsus, the auricle forces pollen basad onto the corbicula. Repetition adds more and more pollen at the distal end of the corbicula, forcing the first pollen collected toward the base of the tibia and ultimately filling the entire corbicula with pollen, which may also be patted from the outside by the ipsilateral mid basitarsus, as noted in the section on Type I Apid Pollen Manipulation. It seems possible that the latter movement may also add some pollen directly from the mid legs to the corbiculae. In both *Apis* and *Bombus*, however, pollen loads composed of different colored pollens from different flowers show that the material is added from the apex of the tibia (Buttel-Reepen, 1915).

Because the published information on *Bombus* is largely presented only by indicating the similarity to *Apis*, R.J. made observations and moving pictures of workers of *B. pennsylvanicus* collecting pollen from *Cassia*. While incomplete, these studies generally verify and supplement the observations made early in the century by Sladen and Buttel-Reepen. A *Bombus* takes a position ventral side up under an inverted flower, usually hanging by its forelegs, sometimes with the midlegs also on the flower. This is clearly a special position for extracting pollen from flowers like those of *Cassia* with tubular anthers. The forelegs do not perform their usual pollen-collecting function and the mid and hind legs are probably freer than usual for pollen-manipulation movements usually performed in flight. The hanging bee produces rhythmic buzzing sounds—vibrations which no doubt release the pollen through the openings in the apices of the anthers (Michener, 1962; Wille, 1963). The pollen falls onto the underside of the bee and especially onto the venter of the abdomen.

While the bee is hanging from the flower, the hind legs (probably under sides of basitarsi but possibly the rastella) sweep back and forth (scraping or rubbing, we cannot say which), transversely, synchronously, removing pollen from the abdominal sterna. In each such movement, as they approach the midventral line of the abdomen, the distal parts of the tarsi meet and interfere with the process. The result is a longitudinal, midventral line of pollen, not swept up by the basitarsi or tibiae.

While still hanging from the flower, the bee performs at least five movements with the middle legs. They were observed to occasionally groom a foreleg by flexing so that the foreleg is scraped simultaneously by mid femur and basitarsus. (This familiar movement is presumably functionless for pollen collecting in the context of *Cassia* flowers.) Midlegs more often scrape anteriorly on the dorsum of the thorax and posteriorly on the venter between fore and mid coxae. The latter movement should sweep *Cassia* pollen from the thoracic venter. The middle legs also, one at a time, extend backward, are appressed between the hind basitarsi, then pull forward as the hind legs are straightened backward. This scrapes pollen from the middle basitarsus onto the under sides of the hind basitarsi. (Basitarsi of pollen-collecting individuals of *Bombus cayanensis* had abundant pollen on their under surfaces.—C.D.M.) Finally, midlegs occasionally pat the corbicular pollen loads, usually starting at the basal part of a pollen mass and working toward the distal part.

Bombus in flight were photographed while cleaning the forelegs with the midlegs and the midlegs with the hind legs—movements also seen while bees were hanging from flowers. In addition, film analysis revealed pumping movements of the hind legs like those described for *Apis*. It was verified that the hind basitarsi are not

pressed against one another as during grooming; contact is in the vicinity of the tibiotarsal joint and we believe that the rastellum of each tibia combs pollen from the underside of the opposite basitarsus. This would lead to deposition of pollen on the auricle, which would push it into the distal end of the corbicula, just as in *Apis*.

Contralateral Pollen Packing in Meliponinae. Although Meliponinae lack auricles, most of them have rastella; it was therefore natural to look for contralateral corbicular loading similar to that known for *Apis*. In some species of *Trigona*, contralateral pollen packing is of little importance, at least at the flowers where we made our observations. Thus the hind basitarsi of *Trigona nigerrima* and *pallida* are brought rather close to one another beneath the body during pollen loading, so that the middle legs can be drawn across the outer surfaces of the hind legs, as described in the section on Ipsilateral Type II Pollen Packing. The hind legs may touch one another and make some basad-distad alternate pumping movements. Moving pictures of hovering *T. nigerrima* taken from the rear show occasions when the inner apex of a hind tibia, bearing the comb or rastellum, combs downward over the inner surface of the opposite or contralateral basitarsus, followed by the same movement of the opposite leg. This alternating or pumping movement is probably not important for pollen manipulation in the cases most intensively studied, *Trigona pallida* on *Ipomoea* and *T. nigerrima* on *Hedychium*, for in these cases the pollen was picked up as described above, exclusively by the front legs; little or no pollen got onto the abdomen or hind tarsi. Moreover, pollen was rarely found on the inner sides of the hind basitarsi in the pollen-collecting bees, and when present, there was but little. The pumping movements in these instances were probably cleaning

or self-grooming activity or stereotyped activity that may have importance in pollen manipulation at other kinds of flowers. These species, however, like all others in the subgenus *Trigona* and certain species of the subgenus *Tetragona*, have a large sericeous area, not covered with bristles, on the inner side of the hind basitarsus. Such a basitarsus must be inefficient, compared to that of other Apidae, in brushing pollen from the middle tarsus and therefore in contralateral pollen packing.

The other subgenera of *Trigona*, like other Meliponinae, have the underside of the hind basitarsus fully bristled and it is among such forms that contralateral pollen packing is most likely to occur. As noted above, much pollen was found on the inner sides of the hind basitarsi of *T. (Scaptotrigona) pectoralis* and *T. (Paratrigona)* species collecting pollen on *Baccharis* (?). The species of *Scaura* discussed in the next section must depend largely on contralateral pollen packing. More significantly, there was much pollen on the inner sides of the hind basitarsi of *T. (Cephalotrigona) capitata* and *T. (Paratrigona) impunctata* collecting pollen from *Stylosanthes*, even though this is a small-flowered legume whose pollen was being removed from the flowers by the front tarsi only. Thus, unlike *Scaura* and the bees on *Baccharis*, those on *Stylosanthes* were not getting pollen on the body. Pollen must have been actively transferred to the inner sides of the hind basitarsi.

Behavioral observations, while not decisive, indicated the same conclusion. Pollen collectors of *T. capitata*, at least those with large pollen loads, seem to place the mid tarsi between the hind tarsi while hovering, after visits to one to several flowers. Thereafter distad-basad pumping movements of the hind legs were conspicuous, the inner apices of the tibiae apparently scraping the inner surfaces of the basitarsi. Sometimes, however, the mid

basitarsi appeared to be outside the hind tibia, which (together with the presence of a strong penicillum) suggests that ipsilateral packing also occurs. *T. (Paratrigona) impunctata* is too small for detailed observations while hovering, but it very rarely seems to transfer pollen while resting on a flower. One mid tarsus at a time is extended posteriorly and pulled forward between the two hind basitarsi which are held with their inner surfaces apposed. This movement was seen performed by two pollen-collecting individuals. The only problem in its interpretation is that this is a typical apoid cleaning movement. The observer (C.D.M.) believed that the movement was pollen transferral, but recognized that it could have been merely cleaning of the middle tarsus. It was followed by hovering and pumping movements of the hind legs, suggesting pollen packing.

Aside from the bristles on the inner side of the hind basitarsus, an essential structure for contralateral pollen packing is the rastellum. This is a row of bristles (Fig. 13) along the inner margin of the apex of the posterior tibia. In *Apis* and *Bombus* the rastellum functions to comb pollen off of the inner surface of the contralateral hind basitarsus, and it extends more or less the full width of the tibial apex. In Meliponinae the row of bristles is commonly shorter, being largely posterior to the basitarsal articulation and penicillum, but probably has the same function; the pumping motion of the hind legs involves combing of hind basitarsi by the rastella. The result is accumulation of pollen from the contralateral basitarsus on the apex of the tibia lateral to the rastellum, from which location basitarsal movements combined with the hairs of the auricular area can presumably push pollen basad onto the corbicula, as in the case of ipsilateral pollen packing.

Probably another significant function of the rastellum is as a fence to prevent

the pollen that is transferred to the outer surface of the hind leg from being pushed onto the inner surface in the course of the tarsal movements. Even if, as in the *Trigona pallida* and *nigerrima* which we studied, little or no pollen is coming from the inner surfaces of the hind basitarsi, pollen arriving on the outer side of the tibiotarsal area might leak through and be lost on the inner surface of the hind tibia in the absence of a rastellum.

The Corbicular Load in Meliponinae. Since in both ipsilateral and contralateral pollen-packing movements, pollen is placed at approximately the hind tibiotarsal joint, there must be a mechanism for forcing pollen basad from that area into the corbicula. This mechanism has been described above, and it is reassuring that pollen loads collected from two or three different kinds of flowers by *Melipona fasciata*, *M. favosa*, and *Trigona fimbriata* indicate the existence of such a mechanism. The pollens in all such loads are arranged as though each new kind were added from the distal end of the tibia (Fig. 14), pushing previously acquired pollen basad over the corbicular surface. If successive kinds of pollen were patted onto the surface of the load (Type I), the different kinds would constitute shells one over the other; this is not the case. In other apid subfamilies the auricle of the basitarsus plays an essential role in pushing pollen basad into the corbicula but, as noted before, the Meliponinae have no auricle.

As the pollen mass on the meliponine corbicula enlarges, it is held and supported by the erect hairs of the lower (or anterior) corbicular margin, by the erect "outer penicillum" or parapenicillum of species such as *Trigona pallida*, by the penicillum proper, and by the few curled hairs at the distal end of the posterior margin of the tibia. The long upper (or posterior) fringe of the corbicula in most *Trigona* species, however, does not contain more or less

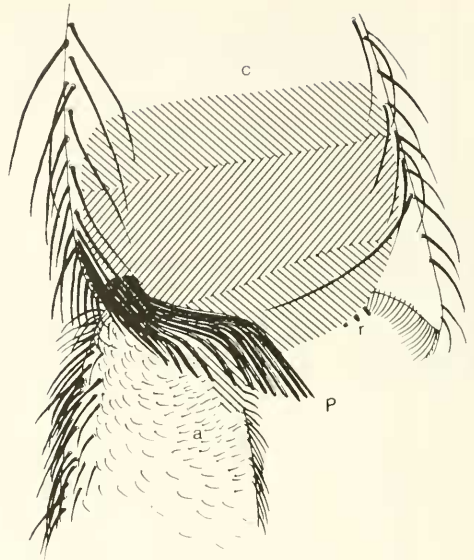


FIG. 14. Apex of tibia and base of basitarsus of *Melipona fasciata*, worker, showing by shading positions of different kinds of pollen. Abbreviations as for Figs. 8-13. Note the pollen on the auricular area behind the penicillum.

erect or curled hairs that enclose a corbicular space, as in *Apis*, *Bombus*, and *Melipona*, but extends posteriorly from the corbicular surface. The pollen mass moves partly out over these hairs (Fig. 9) and the stickiness of the pollen and the liquid incorporated with it holds the pollen both to the corbicular surface and to the posterior fringe of hairs. The pollen mass may be shaped to some degree, or adjusted, by patting movements of the middle legs.

Specializations of Meliponine Pollen Collecting. There doubtless exist, within the behavioral repertoire of various meliponine bees, many modifications of the patterns described above. Wille (1963) describes how *Trigona* f. *fulviventris*, *fuscipennis*, and *silvestriana* cut holes in the tubular anthers of *Cassia biflora* and extract pollen from them with the glossa. Laroca (1970) indicates that *T. spinipes* and *subnuda* behave similarly with similar tubular *Tibouchina* anthers, while *T. fulviventris guianae* cuts the tips off of the *Tibouchina* anthers and then exploits them in the same way.

Similar observations were made by C.D.M. at flowers of another melastomaceous shrub in French Guiana. The flowers are managed differently by different meliponine bees, as follows: *Melipona pseudocentris* curls the body over the group of anthers and buzzes, receiving the pollen from the tubular anthers on the under side of the body as described for other bees by Michener (1962) and Wille (1963). *Trigona impunctata* chews the basal thick parts of the anthers open and extracts pollen with the glossa and fore tarsi. *T. fulviventris guianae* chews off the attenuate distal parts (one third to one half) of the anthers, thus providing an entrance much larger than the small apical pore, and reaches in to extract pollen with the glossa. It then scrapes pollen off of the tongue with simultaneous distad movements of the front basitarsi. A single bee often cuts the apices off of most or all of the anthers in a flower before going on to another.

Trigona species sometimes are gleaners, picking up pollen from corolla surfaces where it falls following visits to anthers by other insects. Although the pollen on the surfaces is usually invisible, bees collect large pollen loads on the corbiculae from these sources. Wille (1963) described such behavior for *T. jaty*, *nigra*, and *testaceicornis* on *Cassia biflora*. On another *Cassia* species C.D.M. and M.L.W. observed that *T. impunctata* visited only the anthers, biting them to get pollen, and *T. pallida* usually did the same thing. The latter species, however, was sometimes also a gleaner, going over the corolla surface below the anthers with the antennal tips down to the surface, the glossa slightly exerted, and the mandibles moving; the fore tarsi swept up the pollen, especially by scraping distad on the glossa, to which it probably stuck because of regurgitated nectar. The rest of the manipulation for both *T. impunctata* and *T. pallida* was as

described previously.

The subgenus *Scaura* of *Trigona*, however, appears to consist of specialized gleaners and visitors to inflorescences consisting of relatively broad surfaces from which pollen can be swept up. These bees have extraordinarily large and hairy hind basitarsi (also hairy middle basitarsi), the principle subgeneric characteristic. Laroca and Lauer (1973) describe pollen collecting by *T. (S.) latitarsis* from the cylindrical inflorescences of *Piper* and from the leaf surfaces beneath the flowers of *Amaranthus*. They describe the use of the hind basitarsi for sweeping up pollen and the rubbing of the hind legs against one another, as described below for *T. longula*. *T. latitarsis* is a minute bee, undoubtedly difficult to observe. From its morphology, we assume that its behavior is similar to that of *T. longula*, a larger species for which we obtained fuller, although still incomplete, information on pollen manipulation.

Trigona longula was visiting a large-flowered *Cassia* species. Only rarely do these bees go to the anthers. When they do, they collect pollen and manipulate it, so far as we could see, like other species of the genus. Nearly all the pollen collecting was by gleaning from petal, bud, or leaf surfaces below the anthers. (Flowers were visited by *Xylocopa*, *Eulaema*, *Euglossa*, and *Centris*, whose buzzing releases pollen, as shown by Wille, 1963.) On such surfaces, there was no noticeable deposit of pollen, but individuals of *T. longula* were able to fill their corbiculae there. In ordinary walking, *T. longula* moves like any other *Trigona* species. On polleniferous surfaces, however, the middle and hind legs are splayed out, the inner surfaces of the basitarsi against the substrate, the hind basitarsi bent forward almost at right angles to the body even though the femora and tibiae are directed backward. With the legs in this position, the bee shuffles

along, dragging the distal part of the abdomen. The tips of the antennae are bent down to the surface; the front legs perform ordinary walking movements. The basitarsi and abdomen must pick up pollen from a rather broad swath as the bee moves along.

A collecting bee frequently stops, raises its abdomen, and while supported by fore and mid legs, scrapes backward over the abdominal surface synchronously with the inner surfaces of the hind basitarsi. Then, beneath the abdomen, it rubs or scrapes the inner surfaces of these basitarsi against one another or the apices of the tibiae in the course of pumping movements of the hind legs. Then the hind legs are lowered for support and the middle legs are brought back usually synchronously to the regions of the apices of the hind tibiae, and the mid basitarsal regions are pulled forward across the outer surfaces of the apices of the ipsilateral hind tibiae. This seems to be a shorter movement than in *T. pallida*, perhaps because the hind legs are not moveable, being used in support, and is oblique, not at right angles to the tibia.

Less often the bee hovers and transfers pollen to the corbiculae by means of leg movements that appear to be similar to those of other *Trigona* species. Details, however, could not be discerned.

Microscopic examination showed that the underside of the apical part of the abdomen (metasomal sterna 4 and 5) has hairs which are curved downward at their apices and thus should readily pick up pollen as the abdomen is dragged forward across the substrate. The inner surfaces of the mid and hind basitarsi are unusually hairy. The outer surface of the broad hind basitarsus is swollen, convex except for the broadly concave auricular area (Fig. 15). The rastellum is long for a meliponine bee.

From these observations we suppose that pollen collected on the inner surface

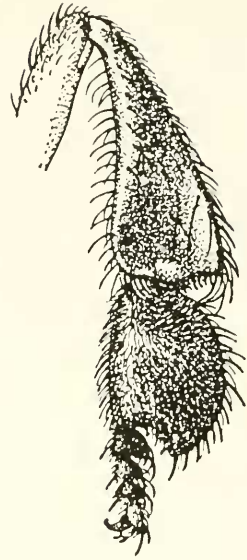


FIG. 15. Hind tibia and tarsus of worker of *Trigona* (*Scutara*) *longula* (modified from Schwarz, 1948).

of the hind basitarsus, both from the substrate and from the abdomen, is combed off that surface by the contralateral rastellum during the observed pumping movements. Pollen should pile up outside of the rastellum; freshly killed pollen collectors had pollen between rastellar bristles and on the outer rastellar surface. Then the concave auricular area, functioning like the auricle in other groups of apids, presumably pushes pollen up into the corbicula. The unusual width of the hind basitarsi, their use and that of the abdomen for pollen collecting, and their general outer convexity so that a concave auricular area can be present, all suggest that contralateral pollen transfer from the inner sides of these basitarsi is more important than in most *Trigona* species. Pollen collected by the front and middle legs is manipulated ipsilaterally, to judge by the observations described above, the penicillum and auricular hairs combing it off and directing it up into the corbicula. We saw no evidence of pollen being removed from the hind legs by the middle legs for transfer to the corbicula, as indi-

cated by Laroca and Lauer (1973) for *T. latitarsis*. As this would involve a forward movement of material, something not seen in grooming or pollen handling behavior of any other bees (Jander, 1976, and in preparation), we suspect an observational error. This would not be surprising considering the minuteness of *T. latitarsis*.

The Euglossini. Pollen collecting by *Euglossa* near *cordata* and *ignita* was observed on small tubular flowers (*Sabicea*) that served also as a nectar source. Hairs on the basal part of the proboscis pull pollen out of the flower. When a bee rears back to withdraw the long proboscis, it places the front tarsi (basitarsi?) on either side of the proboscis, scraping distad several times with the front legs, thus presumably removing pollen from the proboscis.

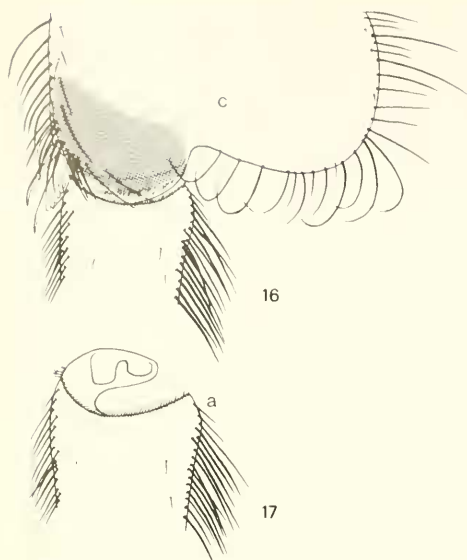
While this is going on the epipharynx, which is extraordinarily long in Euglossini, is exerted and probably adds nectar to the pollen. The proboscis, used for this purpose in other apids, is so long in Euglossini that it could scarcely have this function.

The bee then takes wing and hovers, or rarely grasps a leaf edge with its mandibles and hangs. In either case, the middle and hind legs are freed of their support function, so as to allow pollen manipulation, which is rapid and difficult to observe.

The front legs come back synchronously and apparently the tarsi are scraped by the basitarsi of the flexed middle legs, in the usual way. The latter then moved back synchronously to contact the hind legs. At least part of the time the mid leg pats the corbicula and pollen load on the outside of the ipsilateral hind tibia. Rubbing of the inner surfaces of the hind legs one on the other (pumping motion) was also probably observed; certainly such motions were visible, but contact between the two hind legs could not be verified.

Examination of various females of *Euglossa*, *Euplusia*, and *Eulaema*, killed while collecting pollen, provided more information. The front legs often had a little pollen on the inner surfaces of the basitarsi and less on the tibiae, more on the posterior margins of the inner basitarsal surfaces than elsewhere. The middle legs had similarly distributed pollen, even more predominantly along the posterior margins. Presumably it is the hairs of the posterior parts of the inner surfaces that transfer much of the pollen. On the hind legs, there is little or no pollen on the inner surfaces of the tibiae or tarsi, except that when the pollen load is very large, a thin and broken layer may be present on the inner surfaces.

Whenever the pollen load is of moderate or small size, pollen on the tibiotarsal articular region is limited to the area of the rastellum, and it is on the outer side of the row of bristles, not on the inner side. On the corbicula, any small pollen load is always immediately above the base of the basitarsus, as shown in Figure 16. It must be pushed up to this position by the auricle at the posterior base of the basitarsus. The auricle is present, but unlike that of *Apis* and *Bombus*, it is close against the tibial apex, which is so shaped that the base of the basitarsus rides over the convex tibial apex as the tarsus is moved relative to the tibia. When the pollen load is slightly larger, as in most specimens examined, the small fringe at the anterior base of the basitarsus seems to have played a role (Figs. 16 and 17). This fringe must push pollen among the hairs of the anterior corbicular fringe, for they are surrounded by pollen. Thus if the tarsus is flexed backward, the auricle pushes pollen basad, while if it is flexed forward, the anterior basal fringe does so. There is often some pollen on the outer side of the basitarsus, but this is discontinuous with that on the corbicula except when the pollen load is



FIGS. 16, 17. Structures of hind leg of female of *Euglossa ignita*. 16, Apex of tibia and base of basitarsus, showing by shading location of a small pollen load. 17, Base of basitarsus of same, showing auricle at right and small fringe at upper left that may play a role in moving pollen.

enormous. The movement of the auricle over the bulla or convexity of the tibial apex readily causes this discontinuity.

All this supports the observation that the pollen is applied to the outer surface of the hind leg near the tibio-tarsal joint by the middle leg. Apparently the rastellum serves primarily as a fence to keep the pollen from "leaking" through onto the inner surface. In any event, the rastellum seems to be so positioned that it could comb the contralateral basitarsus only with difficulty. Finally, the huge pollen loads often attained, especially by *Euplusia* and *Eulaema*, are made possible partly by the enormous, posterior expansion of the tibia and could hardly be managed except with adjustment and shaping by the middle legs; some pollen is likely to be added directed to the pollen load in this way.

EVOLUTIONARY CONSIDERATIONS

EVOLUTION OF POLLEN COLLECTING AND TRANSPORT. In the evolution of pollen-

carrying behavior, three successive basic phases can be recognized. If Jander (1976) is correct in considering the crop as the ancestral pollen-carrying structure, the pollen-collecting behavior of *Hylaenus* illustrates the first phase, utilizing structures and behaviors already present in the Sphecidae. *Hylaenus* carries pollen in the crop, collecting it by brushing it off the anthers with the forelegs and then scraping it off each foreleg with a comb on the maxillary galea (Jander, 1976). There is also the possibility that *Hylaenus* eats pollen directly. Moreover, *Hylaenus* can scrape the head with the forelegs and then eat the pollen that was lodged on the head. There are no known *Hylaenus* movements for transferring pollen from the thorax or abdomen to the mouth; such pollen is wasted or the small amounts that stick to the body surfaces are brushed off in a cell, if our knowledge of the repertoire of movements is complete (Jander, in preparation). This *prototypic pollen collecting* of *Hylaenus* persists into the major evolutionary lines of the bees, even though most pollen transport in such bees is external.

In the evolutionary line that led to the families Anthophoridae and Apidae, the original galeal comb of the primitive bees is replaced by a stipital comb (Schremmer, 1972; Jander, 1976), although in many taxa there is no maxillary comb. Within the Apidae a well developed stipital comb is present only in *Bombus* and only *Bombus* is known to have the prototypic pollen-collecting behavior of scraping pollen off of the forelegs with the mouthparts (Jander, 1976). Most other Apidae, including *Apis*, however, have weak stipital combs.

The second phase of the evolution of pollen-collecting behavior led to *eutypical pollen gathering* and transport in a scopa on the hind legs as in the majority of the bees. In eutypical pollen gathering, pollen is transferred from the flower into a scopa

on the hind legs; as noted in the Introduction, it is passed from the anthers to the scopa via the foreleg and the middle leg.

Eutypical pollen manipulation is characteristic (with minor modifications) of at least Colletinae, Halictidae, Andrenidae, and Anthophoridae (including Xylcopinae), of course with the exception of parasitic forms in such groups. Most bees of these groups have hairy bodies on which loose pollen lodges as they work in flowers. Since the middle legs can scrape the thorax as well as the front legs, these bees have movements whereby pollen can be transferred from both the head (as in *Hylaeus*) and the thorax to the scopa. (In many Anthophoridae, scraping movements of the forelegs clean the dorsum of the thorax; Jander, 1976.) Eutypic pollen manipulation should be more efficient than prototypic. However, the eutypical movements still cannot transfer pollen from the abdomen to the scopa. All bees scrape the abdomen with the hind basitarsi to clean it, but pollen on the abdomen must be either lost or merely brushed off in a cell. Type I pollen packing as described above for Apidae is a modification of eutypical pollen transport behavior.

Eutypical pollen gathering has been supplemented by or transformed into a variety of different *metatypic* or *derived pollen gathering* and transport methods. For example, in the Megachilidae the scopa on the hind leg is replaced by one on the ventral side of the abdomen. The pertinent pollen-gathering movements are only partially known (Michener, 1953), but appear to differ from eutypical movements in that the hind legs transfer pollen to the scopa. As they can also brush the abdomen, megachilids should be able to transfer to the scopa for transport, pollen lodging on almost any part of the body. Within the Apidae pollen transfer movements onto the middle leg are also not noticeably different from those of eutypical pollen gathering

(except in the genus *Trigona*). The derived pollen handling features are largely restricted to the interactions between middle and hind legs and pollen packing from the distal end of the tibia. In other words, Type II pollen packing is among the derived methods.

The derived or metatypic movements found in most Apidae include scraping of the abdomen with the inner surfaces of the hind basitarsi and transfer of this pollen to the contralateral corbiculae for transport. Thus, pollen that lodges from flowers on the abdomen, as well as that on the head and thorax, can be used. Derived movements also include transfer of pollen from the middle legs to the inner surfaces of the hind basitarsi. They clearly include the pumping movements of the two hind legs in which the rastellum scrapes pollen off of the contralateral hind basitarsus onto the basal surface of the auricle, and movements of the basitarsus which push pollen basad into the corbicula, which is thus loaded from its distal end. These matters are described in detail above in the section on Type II pollen packing.

EVOLUTION OF CORBICULAE AND THEIR FILLING MECHANISMS. The Apidae have a corbicula on the hind tibia and for all subfamilies of the Apidae it is known that at least sticky material can be transferred into the corbicula in the eutypical behavioral sequence, described above in the sections on Type I Pollen Packing and Transport of Nesting Materials. Hence the corbicula and the eutypical behavioral sequence must have existed in a common ancestor of all Apidae. In the Introduction we suggested the development of the corbicular scopa from the brushy tibial scopa of Anthophoridae. We have two theories, not mutually exclusive, to account for the origin of corbicular transport as contrasted to transport among the hairs of a brushy scopa. One is that a single stroke

of the mid leg is sufficient to empty a corbicula, while several strokes must be needed to empty a brushy scopa. The former should be more efficient. The other theory is that the corbiculae arose in connection with the use of sticky materials for nest construction. It is true that some Megachilidae use resin, mud, and other sticky substances for making cells, but they do not transport such materials in the scopa. It is also true that in the Anthophoridae there are forms such as some *Centris* which transport oil (Vogel, 1974) or mud (Michener and Lange, 1958) in the scopa. However, it seems that it would be nearly impossible to remove highly sticky materials like gums and resins from a brush of dense and usually branched scopal hairs (although Roubik and Michener, in press, indicate that this happens in *Epicharis*). Winston and Michener (1977) therefore suggested that the smooth corbicular surface serves to facilitate removal of such material from the hind legs in the nest, after transport. Most Apidae use the corbicula for transport of both construction materials and pollen. As the corbiculae, according to this theory, are adaptations for the transport of sticky material, it is not surprising that these bees make the pollen into a sticky material too, by the addition of nectar as it is collected.

Because a corbicula can be filled with sticky material in the eutypical fashion and because it is mechanically impossible for a brushy scopa to be loaded with pollen by the highly derived movements found in Apidae, the evolution of the corbicula with its corbicular scopa presumably preceded that of the highly derived behavior and associated structures (rastellum, penicillum) used in pollen packing. This suggestion is supported by the structure of certain African Meliponinae, as described below.

The progenitors of the Meliponinae would not have had such specialized meliponine features as reduced wing venation

and stings, but might well have had the ancestral apid pollen-carrying apparatus. There exist in Africa today groups of meliponines in which the corbicula is fully developed, but in which the tibio-tarsal region lacks (primitively or by loss?) one or both of the special structures that relate to corbicular packing in other Meliponinae. Groups which lack the rastellum are *Trigona* subgenera *Meliplebeia*, *Axestotrigona*, and *Hypotrigona* as well as the genus *Meliponula*. Of these taxa the subgenus *Hypotrigona* has only a weakly developed penicillus which could not function as described in the section on Ipsilateral Type II Pollen Packing. In the other groups listed the penicillum bristles are not so nicely graded in length and curvature as illustrated and described in that section; the penicillum in such cases may well serve only or primarily to support the pollen mass. These same groups have the largest (and flattened) sting sheaths of any Meliponinae; this must be an ancestral feature and thus strengthens the hypothesis that at least in some cases the lack of rastellum and perhaps the weak penicillum are primitive features rather than losses. (These morphological data, but not the interpretations, are from Dr. A. Wille, *in litt.*) Pollen packing in these African groups has not been studied, but it seems almost certain that in *Hypotrigona*, at least, it is like the packing of nest materials and Type I pollen packing described above, i.e., eutypical; the middle legs presumably place sticky pollen directly into the corbiculae. The American subgenus *Trigonisca*, a relative of the African *Hypotrigona*, has relatively feeble penicilla and rastella, and its pollen packing, so far as known, is like that postulated for the ancestral groups, although it may also have in its repertoire the derived pollen-packing methods of most Meliponinae.

POLLEN PACKING IN THE APIDAE. Eutypical pollen manipulation as seen in Apidae in-

volves synchronous movements of the legs of a given pair. Thus the two middle legs even in a *Trigonisca* resting on a petal simultaneously place pollen on the ipsilateral corbiculae. In this respect apids differ from at least many of the non-apid bees, which transfer pollen back to the tibial scopa by movement of one leg at a time. (Observations of non-apids in flight are still needed; their leg movements may then be synchronous.) Movement of both middle and hind legs appears to facilitate pollen transfer to the corbicula, making it easier to get the mid basitarsus to the proper position relative to the hind leg. Simultaneous movement of both mid and hind legs is difficult, however, while the bee uses at least one of these pairs of legs for support. Most apids solve this problem by hovering when employing derived (Type II) pollen-packing methods, so that the legs are freed for the pollen-transferring movements. Such behavior has seemingly been transmitted to males of the Euglossini which use similar movements for transferring scents to the hind tibiae while hovering. Presumably a behavioral pattern that evolved among females was activated in males, which in any case must carry the appropriate genes for it.

Within the Meliponinae, several derived features of pollen manipulation have arisen. Like most Apoidea, meliponines commonly collect pollen with the front tarsi, as well as on other parts of the body when the pollen is loose. Many and perhaps all species of *Trigona* are unusual among bees in that they transfer the pollen from the forelegs onto the thoracic venter and leg bases for temporary storage. It is later picked up by the middle legs (or possibly again by the front legs). We suspect that *Melipona* has lost this behavior for we find no special accumulations of pollen on the mesepisterna and coxae in this genus, nor are there coarse hairs in these areas like those of *Trigona*. *Melipona*

workers move so rapidly that details of their pollen manipulation have eluded us. (Our attempts at observation were mostly made at flowers of *Mimosa*, where the *Melipona* rushes around through the stamens, all parts of its hairy body being dusted with pollen.)

In the species of *Trigona* that we have studied most thoroughly, pollen is transferred to the corbicula by drawing the pollen-bearing middle tarsus across the apex of the ipsilateral hind tibia and base of the basitarsus in such a way that the pollen appears to be picked up and pushed basad onto the corbicula by a structure found only in this subfamily, the penicillum. This behavior resembles eutypical movements in that pollen is transferred to the hind leg by the ipsilateral middle leg, but is derived in that it is not placed directly into the corbicula. In the course of this movement pollen will also be scraped off of the mid basitarsus by hairs of the auricular area of the ipsilateral hind basitarsus.

Pollen also appears to be transferred from inner sides of hind basitarsi to contralateral corbiculae in meliponines. They scrape pollen from the abdomen with the hind basitarsi. Meliponines with a penicillum ordinarily also have a row of bristles across the inner side of the apex of the tibia, the rastellum, which can comb the inner side of the contralateral basitarsus. When large amounts of pollen are combed off of a basitarsus by a rastellum, the pollen accumulates outside the rastellum and can be pushed basad, onto the corbicula, by basitarsal movements which are effective because of the direction of the hairs of the auricular area and perhaps because of the pollen already on those hairs. However, for most meliponines it is probably more important that such pollen can presumably stick to and be carried basad by other pollen transferred to the hind leg by the ipsilateral middle leg.

For many of the commonest species of *Trigona*, the importance of the inner side of the hind basitarsus in transferring pollen seems reduced. In the subgenus *Trigona s. str.* which includes the species that we have studied most carefully and in many species of the subgenus *Tetragona*, there is a large, hairless, sericeous area occupying up to half of the inner basitarsal surface. Accumulations of pollen on this surface have not been seen and are not common even among the hairs on the rest of the surface. These groups are placed among the derived subgenera of *Trigona*. Their rather hairless abdomens and perhaps the nature of the flowers usually visited by them may make brushing of the abdomen of little importance. Probably contralateral pollen transfer is more important in other subgenera in which the under surface of the hind basitarsus is fully covered with bristles of stiff hairs.

Finally for Meliponinae, the gleaning bees of the subgenus *Scaura* represent a noteworthy development, with a concave auricular area or false auricle in the swollen hind basitarsus for pushing pollen upward onto the corbicula. The broad basitarsi as well as the abdominal hairs are used to brush up pollen from flower and leaf surfaces.

In the remaining Apidae (Apinae and the tribes Bombini and Euglossini of the Bombinae) pollen manipulation is also of derived types, but partially different from those of Meliponinae. In the Apinae and Bombini, whose hind tibial and tarsal structure is very similar, pollen from the inner surface of the hind basitarsus is combed off by the contralateral rastellum; it sticks to the tibial apex outside the rastellum, and is then pushed upward onto the corbicula by the strongly developed auricle.

In the Euglossini there is also an auricle although it appears small because of the enormously expanded hind tibia. The auricle is closely appressed to the swelling

or bulla of the tibial apex, so that pollen from the contralateral basitarsus presumably could not be pushed between these leg segments onto the auricle, as in *Apis* and *Bombus*. Moreover, the rastellum does not project mesally in such a way that it could easily comb the contralateral basitarsal hairs, as it does in the other three apid groups. Pollen must therefore be placed on the outside of the hind leg by the middle leg, presumably in the area of the tibiotarsal joint; then it is probably pushed basad into the huge corbicula by the auricle and other basal marginal parts of the basitarsus which slide over the tibial bulla as the basitarsus moves.

If Winston and Michener (1977) have correctly presented the cladistic relationships among apid groups, the Euglossinae must have lost the contralateral pollen transfer and the relatively large auricle characteristic of *Bombus* and *Apis*. The great enlargement of the tibia associated with carrying huge loads of nesting materials and pollen may have had this effect by narrowing the space between the auricle and the swollen tibial apex. Alternatively, the Euglossinae might be, in features of pollen manipulation (as well as in solitary or parasocial behavior), primitive Apidae that, like certain African Meliponinae, have never evolved contralateral pollen transfer. Many more observations of pollen-collecting Euglossinae are needed to settle this problem.

DERIVATION OF POLLEN MANIPULATION FROM SELF-GROOMING MOVEMENTS. Pollen transfer from the foreleg to the middle leg is indistinguishable from the corresponding cleaning movement (Jander, 1976) and is therefore considered homologous to it. The middle leg, with the pollen on its under and inner side, swings backward in cutypical pollen transfer towards the ipsilateral hind leg. The pollen on the middle leg is then pressed into the scopa, and simultaneously the middle leg is pulled

forward and basad relative to the hind tibia, so that the distad-directed hairs of the scopa scrape the pollen off the middle leg. This final scopal loading movement is precisely the opposite of, and presumably derived from, normal self-cleaning behavior, during which bees typically remove dust from the outer side of the hind leg with a distad scraping movement of the ipsilateral middle leg. This cleaning movement, however, is used inside the nest for scraping the collected pollen out of the scopa. (Our remarks above ignore the femoral, trochanteral, coxal, propodeal, and sternal scopal areas of many colletids, halictids, and andrenids, partly for lack of data, but also because in the context of the Apidae it is the tibial scopa that is important.)

Patting of the corbicular pollen load with the middle basitarsus, presumably to adjust and shape the pollen mass, is seen in most or all apids. This movement differs from normal cleaning of the outside of the hind leg and probably from Type I pollen packing movements mainly by suppression of scraping and rubbing components. It is likely that patting is derived from eutypical or Type I pollen-packing movements, which are themselves probably derived from normal cleaning movements. The movements of the mid legs in ipsilateral Type II pollen packing presumably have the same origin.

The derived pollen-manipulating movements of the Apidae also mostly appear to have evolved from cleaning movements. Bees typically clean one middle leg at a time by scraping off foreign particles usually with both but sometimes with only one hind basitarsus. The middle leg is pulled forward, usually between the two hind basitarsi, while the hind legs are pushed backward and downward (Beeken, 1934; Farish, 1972). It is by this very movement that the pollen is transferred from the middle leg to the inner side of the hind basitarsus by Bombini and Apinae and at least some Meliponinae.

After a bee has cleaned its middle legs between the hind basitarsi, it regularly cleans the latter by pressing them flat against each other and then rubbing them with alternating longitudinal pumping movements. During these movements the tarsi are in continuous contact. Dirt is thereby pushed distad because all bristles and hairs on the inner sides of the hind basitarsi point in that direction. [This cleaning movement was observed in all of the 60 species of bees in seven families listed by Jander (1976) and differs from the corresponding cleaning movement of most other Hymenoptera which clean the hind basitarsus by pulling it past the tibiotarsal joint of the contralateral hind leg (Farish, 1972; Wagner, 1959). Normally terminal tibial spurs improve the efficiency of this movement and the so-called strigil of the hind leg of sphecids is its morphological concomitant.] In the pollen manipulation of Meliponinae, Bombini and Apinae an almost typical apoid movement pattern is used when pollen is combed off of the inner surface of the hind basitarsus by the contralateral tibial comb or rastellum. The only known difference between this pollen manipulation and the true cleaning movement is that during the latter the tarsi are pressed against each other while during the former the tarsi are slightly bent apart so that only the distad-moving rastellum contacts the contralateral hind basitarsus. For the final auricular movement that pushes pollen basad from the rastellum into the corbicula, no homologous self-cleaning movement is known.

The peculiar temporary storage of pollen on the thoracic venter and coxae in the genus *Trigona* appears to be the reverse of a widespread cleaning movement in which the forelegs scrape backward on the underside of the thorax, as has been observed in *Nomada vineta*, *Ceratina* (*dupla* or *calcarata*), *Bombus ruderatus* and *Psithyrus variabilis* (R.J.). Further transfer of pollen could easily be mediated by the

middle legs, since backward scraping of the coxae by the middle legs as a component of self cleaning has been seen in *Tricpeolus concavus*, *Anthophora abrupta*, and *Trigona jaty* (R.J.) and has been described for *Apis mellifera* by Beekun (1934).

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LITERATURE CITED

- BASSINDALE, R. 1955. The biology of the stingless bee *Trigona (Hypotrigona) gribodoi* Magretti. Proc. Zool. Soc. London, 125:49-62.
- BATRA, S. W. T. 1966. The life cycle and behavior of the primitively social bee, *Lasiglossum zephyrum* (Halictidae). Univ. Kansas Sci. Bull., 46:359-423.
- BEEKUN, W. 1934. Über die Putz- und Säuberungshandlungen der Honigbiene (*Apis mellifica*). Arch. für Bienenkunde, 15:213-275.
- BELING, J. 1931. Beobachtungen über das Pollensammeln der Honigbiene (*Apis mellifica*). Arch. für Bienenkunde, 12:352-359.
- BRAUE, A. 1913. Die Pollensammelapparate der beinsammelnden Bienen. Jenaische Zeitschr. f. Naturwissenschaften, 50: 1-96, pls. 1-4.
- BUTTEL-RELPEN, H. VON. 1915. Leben und Wesen der Bienen. Braunschweig: Vieweg.
- DODSON, C. H., R. L. DRESSLER, H. G. HILLS, R. M. ADAMS, AND N. H. WILLIAMS. 1969. Biologically active compounds in orchid fragrances. Science, 164:1243-1249.
- EVOY, W. H. AND B. P. JONES. 1971. Motor patterns of the male euglossine bees evoked by floral fragrances. Anim. Behav., 19:583-588.
- FARISH, D. J. 1972. The evolutionary implications of qualitative variation in the grooming behavior of the Hymenoptera. Anim. Behav., 20:662-676.
- HOFFER, E. 1882. Die Hummeln Steiermarks, I. Hälfte. 31. Jahresbericht der Landes-Oberrealschule in Graz. 92 pp., pls. A, 1, and 2.
- IBRA. 1976. Bibliography No. 16. Annotated bibliography on propolis. International Bee Research Association.
- JANDER, R. 1976. Grooming and pollen manipulation in bees (Apoidea): the nature and evolution of movements involving the foreleg. Physiol. Entom., 1:179-194.
- LAROCA, S. 1970. Contribuição para o conhecimento das relações entre abelhas e flores: coleta de pólen das anteras tubulares de certas Melastomataceae. Rev. Floresta [Curitiba, Brazil], 2: 69-74.
- LAROCA, S. AND S. LAUER. 1973. Adaptação comportamental de *Scaura latitarsis* para coleta de pólen. Acta Biol. Paraná, 2:147-152.
- LEGGE, A. P. AND B. BOLE. 1975. Variations in the single hair of the honeybee corbícula. Jour. Apicult. Res., 14: 75-78.
- MAIDL, F. 1934. Die Lebensgewohnheiten und Instinkte der staatenbildenden Insekten. Wien: F. Wagner.
- MAURIZIO, A. 1968. La recolte et l'emmagasinage du pollen par les abeilles, pp. 168-173. In: Traité de Biologie de

- l'Abeille, R. Chauvin Ed., Tome III. Paris: Masson.
- MEYER, W. 1953. Beobachtungen und Versuche über den Transport und die Verwendung von dargebotenem Wachs der Honigbiene. Zeitschr. Bienenforsch., 2:147-157.
- . 1954. Die "Kittharzbiene" und ihre Tätigkeiten. Zeitschr. Bienenforsch., 2:185-200.
- . 1956. "Propolis bees" and their activities. Bee World, 37:25-36.
- MICHENER, C. D. 1944. Comparative external morphology, phylogeny, and a classification of the bees (Hymenoptera). Bull. Amer. Mus. Nat. Hist., 82:258-326.
- . 1953. The biology of a leafcutter bee (*Megachile brevis*) and its associates. Univ. Kansas Sci. Bull., 35: 1659-1784.
- . 1962. An interesting method of pollen collecting by bees from flowers with tubular anthers. Rev. Biol. Tropical, 10:167-175.
- . 1974. The social behavior of the bees. Cambridge: Harvard Univ. Press.
- AND R. B. LANGE. 1958. Observations on the ethology of neotropical anthophorine bees. Univ. Kansas Sci. Bull., 39:69-96.
- AND A. WILLE. 1961. The bionomics of a primitively social bee, *Lasioglossum inconspicuum*. Univ. Kansas Sci. Bull., 42:1123-1202.
- PARKER, R. L. 1926. The collection and utilization of pollen by the honeybee. Cornell Univ. Agr. Expt. Sta. Mem., 98:1-55.
- RIBBANDS, C. R. 1953. The behavior and social life of honeybees. London: Bee Research Assn. Ltd.
- ROBERTS, R. B. 1969. Biology of the genus *Agapostemon* (Hymenoptera: Halictidae). Univ. Kansas Sci. Bull., 48: 689-719.
- RÖSCH, G. A. 1927. Beobachtungen an Kittharz sammelnden Bienen. Biol. Zbl., 47:113-121.
- ROUBIK, D. W. AND C. D. MICHENER. (in press.) The seasonal cycle and nests of *Epicharis zonata*, a bee whose cells are below the wet season water table. Biotropica.
- SAKAGAMI, S. F. AND J. M. F. DE CAMARGO. Cerumen collection accompanied by thieving and attacking in a stingless bee *Nannotrigona* (*Scaptorigona*) (sic) *postica* (Latreille), with a consideration of territoriality in social insects. Rev. Biol. Tropical, 12:197-207.
- SCHREMER, F. 1972. Der Stechsaugrüssel, der Nektarraub, das Pollensammeln und der Blütenbesuch der Holzbiene (*Xylocopa*). Zeitschr. Morph. Tiere, 72:263-294.
- SCHWARZ, H. F. 1948. Stingless bees (Meliponidae) of the western hemisphere. Bull. Amer. Mus. Nat. Hist., 90:i-xvii + 1-546.
- SLADEN, F. W. L. 1911. How pollen is collected by the social bees, and the part played in the process by the auricle. British Bee Jour., 39:491-493.
- . 1912a. The humble-bee. London: McMillan & Co.
- . 1912b. How propolis is collected. Some further notes on pollen-collecting. Gleanings in Bee Culture, 40:335-336.
- SNODGRASS, R. E. 1956. Anatomy of the honey bee. Ithaca: Cornell Univ. Press.
- VOGEL, S. 1963. Das sexuelle Anlockungsprinzip der Catantopiden- und Stenobothriden-Blüten und die wahre Funktion ihres sogenannten Futtergewebes. Österreich. Bot. Zeitschr., 110:308-337.
- . 1966. Parfümsammelnde Bienen als Bestäuber von Orchidaceen und *Gloxinia*. Österreich. Bot. Zeitschr., 113: 302-361.
- . 1974. Ölblumen und ölsammelnde Bienen. Tropische Subtrop. Pflanzenwelt [Mainz], 7:1-267.
- WAGNER, M. 1959. Die Putzhandlungen der Hymenopteren. Dissertation: University of Munich.
- WILLE, A. 1963. Behavioral adaptations of bees for pollen collecting from *Cassia* flowers. Rev. Biol. Tropical, 11:205-210.
- WINSTON, M. L. AND C. D. MICHENER. 1977. Dual origin of highly social behavior among bees. Proc. Nat. Acad. Sci., U.S.A., 74:1135-1137.